

## SPLIT SKIPPERS: MEXICAN GENUS *POANOPSIS* GOES IN THE *ORIGENES* GROUP—AND *YVRETTA* FORMS THE *RHESUS* GROUP—OF *POLITES* (HESPERIIDAE)

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**ABSTRACT.** Genitalia show that the montane Mexican genus *Poanopsis* Godman fits snugly within the *origenes* group of *Polites* Scudder and that *Yvretta* Hemming constitutes a new species group of *Polites*. Relationships have been masked in part by evolutionary reduction and loss of various characters. The *origenes* group, with the northern superspecies *Polites mystic* (*P. mystic* (Edwards) + *P. sonora* (Scudder)), the intermediate linking species *P. origenes* (Fabricius), and the southern sister species *P. puxillius* (Mabille) **new combination** and *P. pupillus* (Plötz) **new combination**, extends from the width of southern Canada to southern Mexico. The *rhesus* group of *Polites*, with *P. rhesus* (Edwards) and the sister species *P. carus* (Edwards) and *P. subreticulata* (Plötz) (**new combinations**, all), extends from southern central Canada to Panama. Geographic distributions of species within these groups (and in the *themistocles* and *vibex* groups of *Polites*, as well) still strongly reflect allopatric speciation.

**Additional key words:** genitalia (male and female), variation, generic limits, character reduction and loss, speciation (allopatric).

In dealing with biodiversity, systematists divide and conquer. Formally described divisions assume a life of their own. The longer they live and the more we use them, the sounder they seem. Sometimes we get so accustomed to overly fine divisions that we cannot see the forest for the trees. The American genus *Polites* Scudder is one such forest, a good bit larger and denser than we thought.

Once upon a time, Godman (1900) created *Poanopsis* for a small, brown, high montane, Mexican skipper, *Pamphila puxillius* Mabille, which he made the type of his monotypic new genus. He observed that *puxillius*, with its short, broad wings, looks like *massasoit* Scudder, the type of the genus *Poanes* Scudder (hence the name *Poanopsis*), but differs conspicuously in having an oblique stigma on the forewing of the male from the origin of vein 3 to vein 1. Godman (1900:pl. 93, fig. 40—my Fig. 1) illustrated the male genitalia of *Poanopsis puxillius* without comment. In mid century, Evans (1955) added a similar Mexican skipper, *pupillus* Plötz (= *catahorma* Dyar), to *Poanopsis*, caricatured the male genitalia of both species, and set *Poanopsis* next to *Poanes*, eight genera removed from *Polites*. However, genitalia show that both species of *Poanopsis* belong in one of the species groups of *Polites*.

*Polites* is a familiar, widespread, New World genus, stretching from Canada to central Argentina, from Atlantic to Pacific coasts in both Americas, and through much of the West Indies. On the basis of genitalic

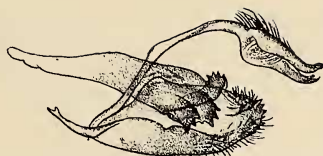


FIG. 1. Male genitalia of *Polites puxillus* (minus left valva) in left lateral view (ex Godman 1900:pl. 93, fig. 40). This figure presents the inner surface of the right valva whereas those that follow present the outer surface of the left valva. The specimen is "from the high tablelands of MEXICO."

and stigmal characters, MacNeill (1993) recognized four subdivisions: the *themistocles* group, the *origenes* group, the *vibex* group, and *Polites baracoa* (Lucas). He pointed out that, within groups (the *themistocles* group in particular), genitalia may be so conservative and so individually variable that differences between species blur but that, paradoxically, superficial color pattern will distinguish some of the genitalic look-alikes.

#### THE ORIGENES GROUP OF *POLITES*

The *origenes* group contains the eastern and central North American *Polites origenes* (Fabricius) plus the continent-spanning and largely allopatric sisters *P. mystic* (Edwards) and *P. sonora* (Scudder), all of which show some internal differentiation. From an evolutionary perspective, *P. mystic* and *P. sonora* can be considered a superspecies (see Stanford & Opler 1993:74, 75 for maps that more or less reflect the mutual geographic replacement of these two similar species, and see Burns 1964, 1983 for detailed analyses of superspecies in other American skippers). The *origenes* group ranges from Canada to the southern United States and, disjunctly, to higher elevations in the Sierra San Pedro Mártir of Baja California Norte, Mexico. Now, with *Polites puxillus* **new combination** and *Polites pupillus* **new combination**, it jumps from three to five obvious species and from the southern United States to southern mainland Mexico. Though these five species vary greatly in facies, they are genitally close, especially in males.

To be sure, male genitalia are grossly similar throughout the genus *Polites* (see figures in Scudder 1889, Skinner & Williams 1924 [or Lindsey et al. 1931], MacNeill 1993). Of all parts, the aedeagus is most generally useful in clustering species. Its accessories at once stamp the *origenes* group: the paired, toothed titillators are large, boldly dentate plates, something like semicircular saws (Figs. 1–5), extending downward from the lower part of the flared, distal end of the aedeagus (Figs. 1, 3, 5); and the lone cornutus is a rolled scroll bearing a crown of thorns (Figs. 2–5). In all other *Polites* the paired, toothed titillators assume



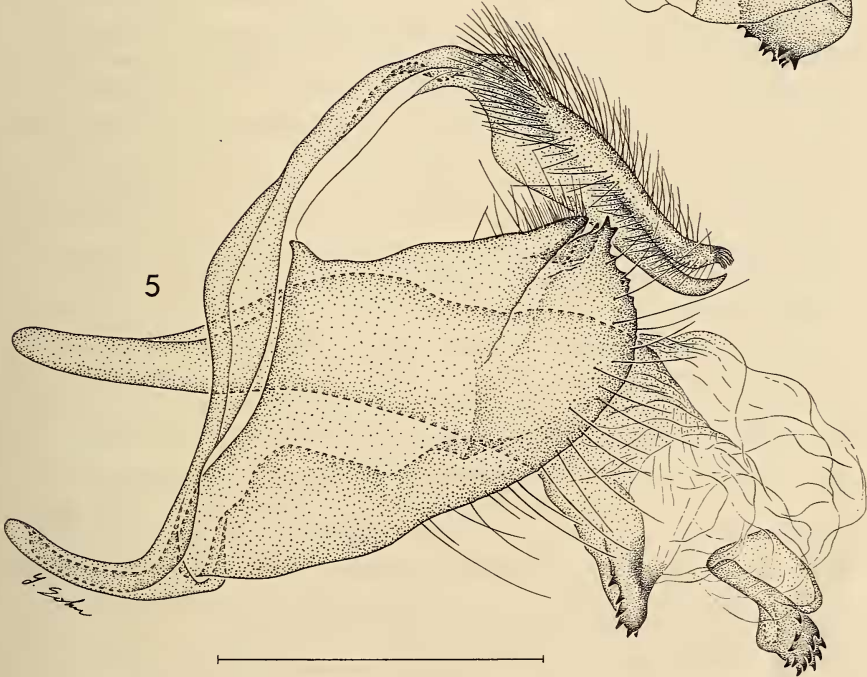
FIGS. 2, 3. Male genitalia of *Polites puxillus* from 28 mi (45 km) E El Salto, 8400 ft (2560 m), Durango, MEXICO, 6-7 August 1972, Viers & MacNeill [genitalia dissection number X-2652] (USNM). Scale = 1.0 mm. **2**, Tegumen, uncus, tip of gnathos, both valvae, both titillators (each with four teeth), and the single cornutus (like a rolled scroll bearing a crown of thorns)—all in posterior view; **3**, Complete genitalia (minus right valva, right titillator, and juxta) in left lateral view, with vesica everted.

FIGS. 4, 5. Male genitalia of *Polites pupillus* from Sierra de Guerrero, MEXICO, July 1913, R. Müller [X-2699] (USNM) (type of *Amblyscirtes catahorma* Dyar). Scale = 1.0 mm. **4**, Tegumen, uncus, tip of gnathos, both valvae, both titillators (left with 10 teeth, right with 8), and the single cornutus (like a rolled scroll bearing a crown of thorns)—all in posterior view; **5**, Complete genitalia (minus right valva, right titillator, and juxta) in left lateral view, with vesica everted.

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very different shapes, come from the upper (rather than lower) part of the distal end of the aedeagus, and, if they extend anywhere, extend backward (not downward); decorated cornuti number two or three (instead of one) and suggest thorny scrolls only in the *vibex* group (where the aedeagus sports a unique, midventral, caudally-directed prong).

The distal end of the uncus, which is divided, is bent farther dorsad in the *origenes* group (Figs. 1, 3, 5) than in any other group of *Polites*.

Female genitalia in *Polites* present less of a generic gestalt, varying more both within and between groups—and, to some degree, in parallel—so that group characterization is not as simple. In the *origenes* group (also in the *vibex* group, but in no others) the apophyses anteriores join the lamella postvaginalis via continuously sclerotized bands (Figs. 6–9). In the *origenes* group (also in *P. baracoa*) sclerotization of the lamella postvaginalis is intermediate (*P. puxillius* [Figs. 6, 7], *P. pupillus* [Figs. 8, 9], and *P. origenes*) to extensive (superspecies *P. mystic*) rather than limited (as it is in the *themistocles* group [MacNeill 1993] and in the *vibex* group [where the lamella postvaginalis carries a unique, midventral, short, sclerotized, finely spined keel]). In the *origenes* group sclerotization of the ductus bursae is partial and posterior; but it may be ventral only (superspecies *P. mystic*), ventral and lateral (*P. pupillus* [Figs. 8, 9]), or ventral, lateral, and, in a very narrow band, dorsal (*P. puxillius* [Figs. 6, 7], *P. origenes*, and, at times, vaguely, *P. pupillus*)—always with a longitudinal, midventral groove (Figs. 6–9) or break in the sclerotization. (Sclerotization of the ductus bursae is partial, posterior, but 360° and broadly ringlike [though midventrally weak] in the *vibex* group; partial, lengthy, mostly ventral but also somewhat lateral [resembling a long, essentially ungrooved, scoop] in *P. baracoa*; and complete, extending more or less the entire length of the ductus bursae and running all the way around, usually with a strong middorsal groove and a ventral pouch, in the *themistocles* group [MacNeill 1993].)

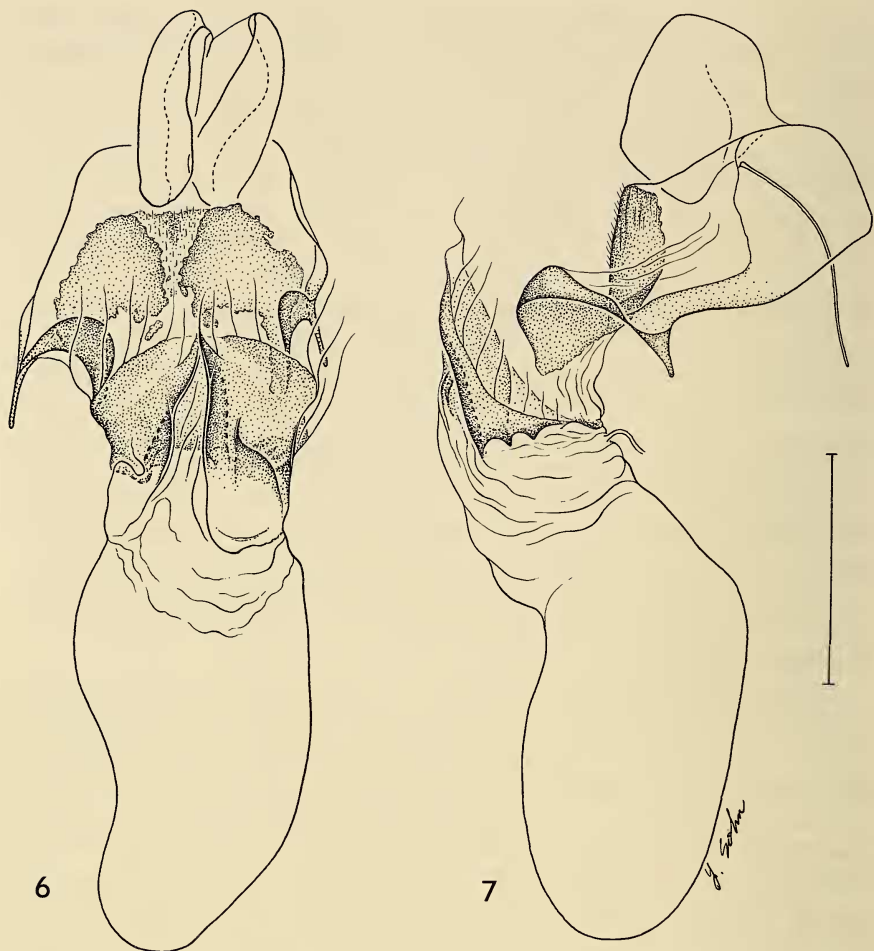
While the northern major differentiates of the *origenes* group of *Polites* (*P. origenes* and superspecies *P. mystic*) are widely known, repeatedly shown in the rising tide of North American butterfly books, and readily separable superficially, the southern differentiates (*P. puxillius* and *P. pupillus*) are not and must be treated here. Whereas in both sexes of *mystic* and *sonora* and in males of *origenes* extensive yellow to yellow-orange brightens the dorsal wing surface, in females of *origenes* and in both sexes of *puxillius* (Figs. 23, 24) and *pupillus* (Figs. 25, 26) the wings above look basically brown (with a variable set of small, pale spots [yellowish in *origenes*, white in *puxillius* and *pupillus*]). Wingshape is sexually dimorphic in the northern three species but not in the southern two: in *mystic*, *sonora*, and *origenes* the wings of males are narrower and more pointed, those of females, broader and

rounder; but in *puxillius* and *pupillus* the wings are broad and round in both sexes (Figs. 23–26). So, with respect to both color and wingshape, *puxillius* and *pupillus* tend to resemble females of *origenes*.

In the two Mexican species, wing spots, which are white, are expressed better by *pupillus* (Figs. 25, 26) than by *puxillius* (Figs. 23, 24). Forewing spots of *pupillus* look whiter and brighter partly because, in some to most of them, some scales stand up from the surface of the wing so as to let light through. In *puxillius* all the white scales lie flat against the wing so that all spots are opaque, none hyaline. Usually, *pupillus* develops a full set of forewing spots—in spaces 1b, 2, 3, 4, 5, 6, 7, 8, and the cell (Figs. 25, 26)—but *puxillius* rarely does, almost always dropping the one or two spots in space 1b (Figs. 23, 24), often skipping those in spaces 4 and 5, as well as that in 8 (Fig. 23), and, in one male examined, losing all but spots 3 and 6. At least some hindwing spots (which are opaque) appear dorsally in *pupillus* (usually spots 2 to 6) (Figs. 25, 26) while none really do in *puxillius* (Fig. 23) (at most, there may be a suggestion of a spot in space 3—see Fig. 24). Ventrally, where spot development is better, up to a full set may surface in *pupillus*—in spaces 1c, 2, 3, 4, 5, 6, 7 (rare) and the cell (Figs. 25, 26); in *puxillius* ventral expression runs the gamut from all except the rare spot 7 (Fig. 24) to nothing whatsoever.

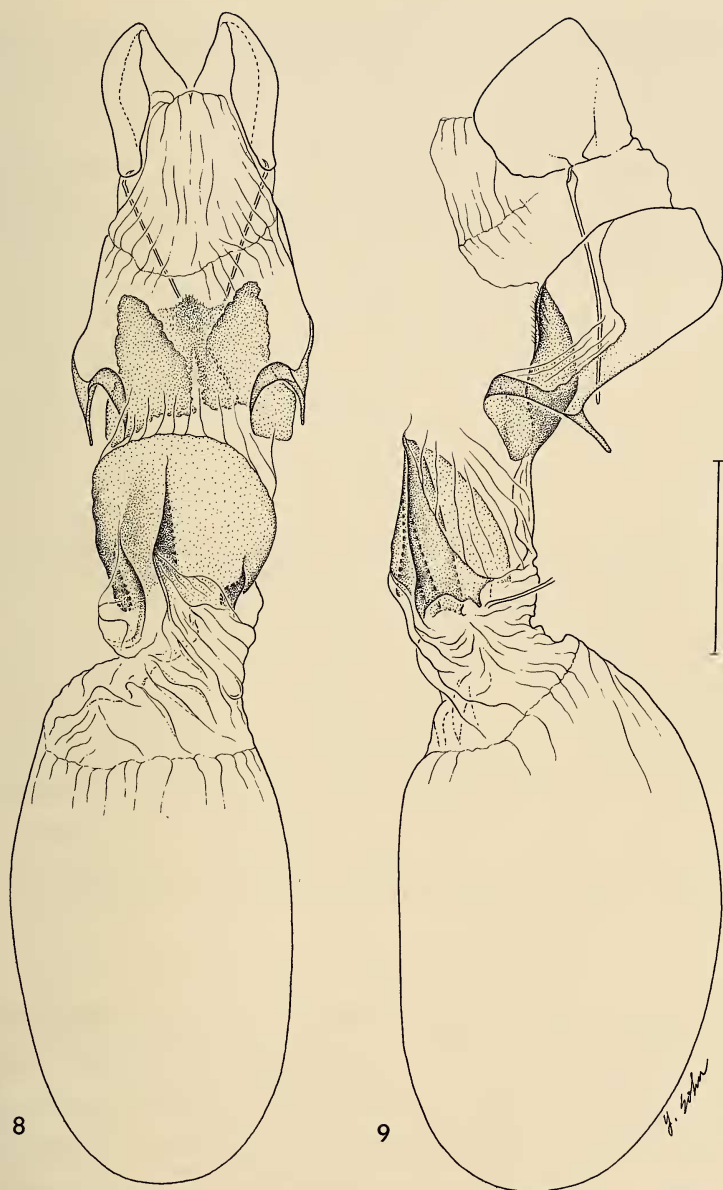
As for real interspecific differences in the conservative but individually variable male genitalia, titillator teeth are fewer in *puxillius* (Figs. 1–3), varying from 4 to 6 (usually 4) on each of the paired titillators, and commoner in *pupillus* (Figs. 4, 5), where they vary from 6 to 10 (usually 7 or 8). The valva of *puxillius*, in lateral view (Fig. 3), is more tapered distally along its ventral margin and hence not as broad (from top to bottom) at its distal end as it is in *pupillus* (Fig. 5). (Evans does not mention these differences; yet once you know what to look for, you can detect both of them in his [1955:pl. 78, M.21.1, M.21.2] genitalic cartoons.) In posterior view, the lower part of the divided distal end of the valva usually forms more of a U in *puxillius* (Fig. 2) than it does in *pupillus* (Fig. 4). Though conspicuous in the specimens figured, this difference almost vanishes when certain variants are compared. The greater valval height of *pupillus*, evident in lateral view, usually shows too in posterior view as a ventral, vertical extension below the U (compare Fig. 4 with Fig. 2).

One interspecific difference in the highly variable female genitalia crept into the foregoing group comparisons: the incomplete sclerotization of the ductus bursae (mainly ventral and lateral) continues dorsally to form a narrow but unmistakable sclerotized ring around the ductus in *puxillius* (Figs. 6, 7) but not—or, at best, very weakly—in *pupillus* (Figs. 8, 9). In addition, the sides of the midventral groove in



FIGS. 6, 7. Female genitalia of *Polites puxillus* from 25 mi (40 km) W Durango, Durango, MEXICO, 5 August 1972, MacNeill & Viers [X-2653] (USNM). Scale = 1.0 mm. 6, Ovipositor lobes (retracted), eighth tergite with apophyses anteriores (sclerotically connected to the lamella postvaginalis of the sterigma), sterigma, and bursa copulatrix in ventral view; 7, The same, plus the right apophysis posterioris and part of the ductus seminalis, in right lateral view.

the ductal sclerotization are more divergent anteriorly in *puxillus* (Fig. 6) than in *pupillus* (Fig. 8), and the sclerotization itself is more fluted in *puxillus* (Figs. 6, 7) than it is in *pupillus* (Figs. 8, 9). The lateral part of the ductal sclerotization (which is more extensive on the left side than on the right—see Figs. 7, 9) is more extensive on both sides in *pupillus* than it is in *puxillus*; so it better hides the roof of the



FIGS. 8, 9. Female genitalia of *Polites pupillus* from 34 mi (55 km) SE Acatlán, 6000 ft (1830 m), Puebla, MEXICO, 9 July 1952, E. E. Gilbert, C. D. MacNeill [X-3198] (MacNeill collection). Scale = 1.0 mm. 8, Ovipositor lobes (exserted) with apophyses posteriores, eighth tergite with apophyses anteriores (sclerotically connected to the lamella postvaginalis of the sterigma), sterigma, and bursa copulatrix in ventral view; 9, The same, plus part of the ductus seminalis, in right lateral view.



midventral groove in lateral view in *pupillus* (Fig. 9) than in *puxillius* (Fig. 7). Again in lateral view, the roof of the midventral groove is convex in *puxillius* (Fig. 7) but straight in *pupillus* (Fig. 9). All these interspecific differences are rather subtle.

*Polites pupillus* is larger than *P. puxillius*. In each species the forewing of the female averages about one mm longer than that of the male, and in each sex the forewing of *pupillus* averages about one mm longer than that of *puxillius*:

	sex	mean	range	n
<i>puxillius</i>	♂	13.6	12.6–14.4	9
	♀	14.9	14.0–15.6	13
<i>pupillus</i>	♂	14.8	13.5–16.2	16
	♀	15.7	15.0–16.4	5

The number of segments in the nudum of the antenna ranges from 11 to 13 in *puxillius* (mean = 12.2, n = 21) and from 11 to 14 in *pupillus* (mean = 12.8, n = 20). In both species nudum segments are evenly split between the body of the club and the apiculus.

Although both species are montane, *P. puxillius* is higher, altitudinally tighter (recorded from 8000 to 8500 ft [2440–2590 m]), and less widely distributed (Durango [Fig. 10]—to as far south as Guerrero according to Godman 1900, Hoffmann 1941). *Polites pupillus* extends from 4200 to 7500 ft (1280–2285 m) and from Sonora and Sinaloa to Colima, Puebla, Guerrero, and Oaxaca (Fig. 10). So far as known, flight times are similar: dates on specimens of *puxillius* examined run from 18 July to 11 August; on *pupillus*, from 3 July to 8 August.

#### THE RHESUS GROUP OF *POLITES*

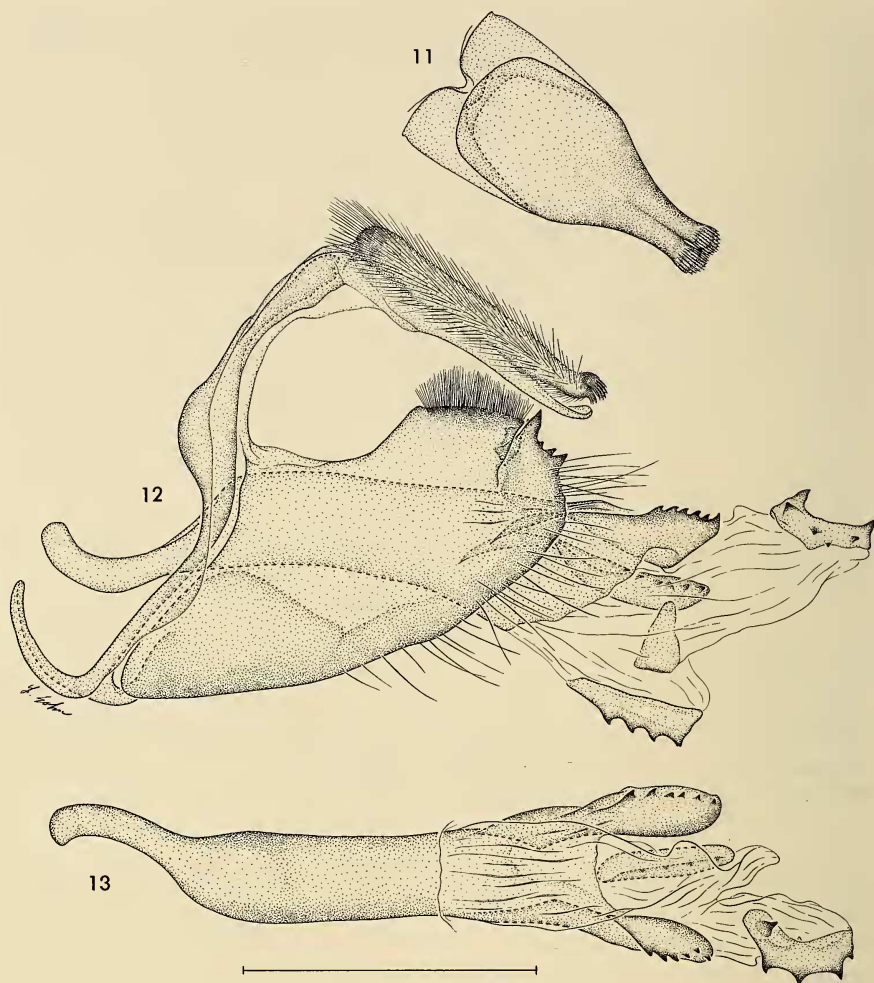
The *rhesus* group of *Polites* comprises at least three species (usually treated as two) that collectively range from the grasslands of southern Saskatchewan and Alberta, Canada, through the western Great Plains, southern Rocky Mountains, and southwestern United States, through Mexico and Central America, to the middle of Panama. Although Godman (1900:474) noted that “the structure of the genitalia of the males is very similar in the two species” when he put them in his new genus *Chaerephon*, he did not see the great similarity between their genitalia (Godman 1900:pl. 93, figs. 4 and 7—my Figs. 15, 16) and those of what he called *Thymelicus vibex* (pl. 93, fig. 14) and *Poanopsis puxillius* (pl. 93, fig. 40—my Fig. 1), which were on the same plate and which now are both in *Polites*. Likewise, Skinner and Williams (1923) figured the



FIG. 10. Geographic distribution (based on plottable material examined) of Mexican sister species *Polites puxillus* (triangles) and *P. pupillus* (dots).

male genitalia of the two U.S. species of *Chaerephon* and then (1924) those of nine U.S. species of *Polites* without seeing how remarkably close they are. Enamored of names, Hemming (1935) saw that *Chaerephon* Godman is a junior homonym and replaced it with *Yvretta*. Commenting that its “genitalia [are] very like those of *Polites*,” Evans (1955:315) still set *Yvretta* next to *Hylephila*, six genera removed from *Polites* (and 21 genera from *Poanopsis*). MacNeill (1993:177) observed that “male genitalic similarities suggest that the nearest relatives of *Polites* are the genera *Yvretta* Hemming, *Hylephila* Billberg, and *Wallengrenia* Berg.” I am going much further by reducing *Yvretta* to a new species group of *Polites*, with the species *Polites rhesus* (Edwards), *P. carus* (Edwards), and *P. subreticulata* (Plötz) (**new combinations**).

Like all other elements of the male genitalia, the aedeagus in the *rhesus* group has that *Polites* look: anteriorly narrow, it at least doubles in size (in lateral view) with the entry of the ductus ejaculatorius and more or less flares at the elaborate distal end, which flaunts a pair of



FIGS. 11–13. Male genitalia of *Polites subreticulata* from Coatepec, Veracruz, MEXICO, October 1910, R. Müller [X-3499] (USNM). Scale = 1.0 mm. 11, Tegumen and uncus (gnathos hidden) in dorsal view; 12, Complete genitalia (minus right valva and juxta) in left lateral view (left titillator more dorsal and more tightly dentate than right), with vesica everted showing all three cornuti (two dentate [upper one curved, lower one straight] and one without teeth); this individual somewhat malformed anteriorly: saccus curved sharply upward, aedeagus bent to right, and bottom of tegumen not curved ventrad near juncture with vinculum (compare Fig. 14); 13, Aedeagus in dorsal view (left titillator more tightly dentate than right), with vesica everted (only the two dentate cornuti visible).

toothed titillators as well as toothed cornuti in the vesica (Figs. 1, 3, 5, 12–16, and figs. 11–19 in MacNeill 1993).

In the *rhesus* group, the paired, toothed titillators come from the upper part of the distal end of the aedeagus, extend backward with



FIG. 14. Male genitalia (digital image) of *Polites rhesus* from Sapillo Creek Valley, 5800 ft (1770 m), 12 mi (19 km) N Pinos Altos, Grant Co., New Mexico, USA, 28 May 1959, J. M. & S. N. Burns [X-2712] (USNM). Complete genitalia in left lateral view (right titillator out of focus and toothless cornutus hidden), with vesica everted showing both dentate cornuti (upper one curved, lower one straight).

one twist along their narrow length, and then expand distally into the dentate portion, with 3 to 7 teeth (usually 5) on the left titillator and 4 to 7 teeth (usually 4, 5, or 6) on the right (Figs. 12–16). The teeth are closer together on the left titillator than they are on the right one (Figs. 12, 13). In another asymmetric touch, the left titillator is more dorsal than the right one (Fig. 12). Like the number of teeth, the length of the titillators varies individually instead of interspecifically or geographically: in each species of the *rhesus* group, the titillators may be equal (Figs. 12, 13, 15), or the left one may be a little to a lot shorter than the right. Two of the three cornuti are conspicuous and tentlike—one essentially straight, the other slightly to very curved, each with 3 to 6 teeth, which are closer together on the straight cornutus than they are on the curved one (Figs. 12–14). The third cornutus is very inconspicuous, amounting to nothing but a bit of lightly sclerotized vesica (Fig. 12).

Right down to the titillators and cornuti, the aedeagus of the *rhesus* group recalls that of the *themistocles* group (compare Figs. 12–16 with figs. 11–19 in MacNeill 1993 and see MacNeill's diagnosis of the *themistocles* group). Some variation is less rampant in the *themistocles* group, even though that group is larger: in *P. themistocles* (Latreille) itself, the two titillators are always the same length (fig. 19 in MacNeill 1993); and in what I consider the *peckius* subgroup comprising *P. peckius* (Kirby), *P. sabuleti* (Boisduval), *P. norae* MacNeill, *P. draco* (Edwards), and *P. mardon* (Edwards), the left titillator is always much shorter





FIGS. 15, 16. Male genitalia of *rhesus* group *Polites* (minus left valva) in left lateral view (ex Godman 1900:pl. 93, figs. 4, 7). **15**, *Polites subreticulata* from MEXICO or GUATEMALA (aedeagus artificially rotated so that the left titillator is lower than the right whereas the reverse is really true); **16**, *Polites rhesus* from Milpas, 5900 ft (1800 m), Durango, MEXICO (tegumen plus uncus artificially twisted so that the underlying gnathos and the gap between it and the uncus fail to show).

than the right (figs. 11–18 in MacNeill 1993). Throughout the *themistocles* group, the third, lightly sclerotized cornutus (inconspicuous in the *rhesus* group) is elongate and suggestive of a scouring pad (with a surface that MacNeill [1993] calls “minutely scobinate”). Otherwise, the basic forms and arrangements of aedeagal accessories are closely similar in the *rhesus* and *themistocles* groups (small differences will be evident in the comparison of figures—but a few figures cannot adequately convey individual variation, which tends to weaken such differences). In contrast, forms and arrangements of aedeagal accessories differ sharply (and in different ways) in the *origenes* group (Figs. 1–5), the *vibex* group, and *P. baracoa*.

What aspects of the male genitalia set the *rhesus* group apart? In *Polites* the distal end of the uncus is divided: each of the two uncal tips terminates in a two-layered comb, with extremely close-set tines curving backward and downward in each layer. These “uncal combs” (called “pectines” by MacNeill 1993) are slightly enlarged in the *rhesus* group (Figs. 11, 12, 14, 16), intermediate in the *themistocles* and *origenes* (Figs. 2–5) groups, reduced in the *vibex* group, and absent in *P. baracoa*. There is a sizable gap between the distal end of the uncus and the underlying divided gnathos in the *rhesus* (Figs. 12, 14, 15), *origenes* (Figs. 1, 3, 5), and *vibex* groups, and in *P. themistocles* (fig. 10 in MacNeill 1993)—but not in other members of the *themistocles* group (i.e., the *peckius* subgroup), where the gnathos is up against the bottom of the uncus (figs. 2–9 in MacNeill 1993). There is no gap in *P. baracoa*, either, but for a totally different reason: this species has lost the underlying divided gnathos.

In *Polites* the dorsodistal corner of the valva is split by a small notch (Figs. 3, 5, 12, 14–16, and figs. 2–10 in MacNeill 1993): the dorsal margin of the valva immediately anterior to this notch supports a dense field of more or less dorsally-directed bristles; and the posterior margin of the valva immediately posterior to this notch displays (in lateral view) at least one sizable, dorsally- or dorsocaudally-directed tooth

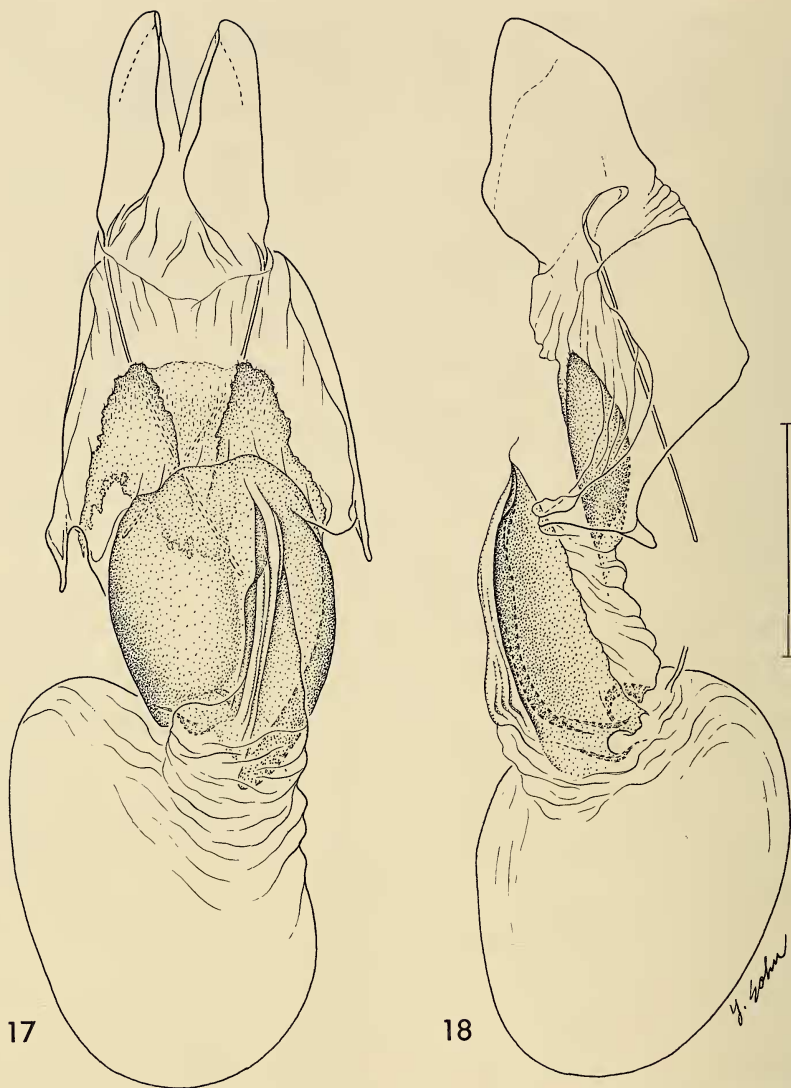
which, in turn, joins one or more teeth (readily visible in posterior view [Figs. 2, 4]) that extend mediad beneath the more or less medially-expanded posterior edge of the dense field of bristles. Medial expansion of the bristled area is least in the *vibex* and *themistocles* groups, strong in the *origenes* group, and greatest in *P. baracoa* and the *rhesus* group. In lateral view this expansion produces a slight hump (in the *origenes* group, Figs. 3, 5) to a very perceptible hump (in *P. baracoa* and the *rhesus* group, Figs. 12, 14) on the dorsal margin of the valva anterior to the valval notch. The posterior edge of the dense field of bristles is without teeth in the *rhesus* group, finely dentate in the *themistocles* group, more coarsely dentate in *P. baracoa* and the *origenes* group (Figs. 2, 4), and most coarsely dentate in the *vibex* group.

About halfway down the posterior margin of the valva (in lateral view) a massive projection extends backward in *P. baracoa* and one or more sizable teeth point backward in the *rhesus* group (Figs. 12, 14–16). This portion of the posterior margin is finely dentate (Figs. 3, 5) to smooth in the *origenes* group and essentially smooth in the *vibex* and *themistocles* groups (figs. 2–10 in MacNeill 1993).

The one or more teeth—visible in posterior view (Figs. 2, 4)—that extend mediad beneath the posterior edge of the dense field of bristles, are conspicuously multiple in the *origenes* group (Figs. 2, 4), in the *vibex* group, in *P. baracoa*, and in *P. themistocles* but are single to inconspicuously multiple especially in the *peckius* subgroup but also, somewhat less consistently, in the *rhesus* group.

The posterior margin of the valva (in lateral view) has more of a “chin”—so looks more squared off—in the *rhesus* group (Figs. 12, 14–16) than in any other group of *Polites*. Certain members of the *origenes* group (*P. mystic*, *P. sonora*, *P. pupillus* [Fig. 5], and some individuals of *P. origenes*) come closest to this well-chinned look. Farthest from it, in a sense, is the *vibex* group because the posterior half of the ventral margin of the valva is narrowly excised.

Female genitalia in the *rhesus* group (Figs. 17–22) are broadly reminiscent of those of the *origenes* group—particularly *P. origenes*, *P. puxillius*, and *P. pupillus* (Figs. 6–9)—except that the apophyses anteriores are not sclerotically connected to the lamella postvaginalis. Sclerotization of the lamella postvaginalis is intermediate, as in *P. origenes*, *P. puxillius*, and *P. pupillus*. Sclerotization of the ductus bursae is partial—mostly ventral and lateral, with a narrow, dorsal extension anteriorly—in *P. rhesus* (Figs. 17, 18) and *P. carus* (Figs. 19, 20), much as in *P. origenes*, *P. puxillius* (Figs. 6, 7), and *P. pupillus* (Figs. 8, 9); but it is virtually complete in *P. subreticulata* (Figs. 21, 22). In all three species of the *rhesus* group, as in all members of the *origenes* group, the ductus bursae has a ventral, longitudinal groove or break. This



FIGS. 17, 18. Female genitalia of *Polites rhesus* from Denver, Colorado, USA [X-3490] (USNM). Scale = 1.0 mm. **17**, Ovipositor lobes (exserted) with apophyses posteriores, eighth tergite with apophyses anteriores (not sclerotically connected to the lamella post-vaginalis of the sterigma), sterigma, and bursa copulatrix in ventral view; **18**, The same, plus part of the ductus seminalis, in right lateral view.

groove is to the right of center in the *rhesus* group (Figs. 17, 19, 21) instead of more or less midventral as it is in the *origenes* group (Figs. 6, 8).

Owing to their overall conservatism and their individual variation,

the male genitalia of the *rhesus* group are not diagnostic at the specific level. But here, as in the *themistocles* group, external color pattern separates species: the underside of the hindwing instantly sets *P. rhesus* (Figs. 27, 28) apart from *P. carus* (Figs. 29, 30) and *P. subreticulata* (Figs. 31, 32). These last two species are much more similar in pattern (so much so that they are mistakenly regarded as subspecies). Color may help in determining unworn specimens: the spots of the upperside are usually creamy to pale yellow in *P. carus* and light to medium yellow-orange in *P. subreticulata*. Although the undersides tend to be creamier in *carus*, yellower in *subreticulata*, they overlap considerably.

It is the female genitalia that best distinguish these species. The ductus bursae is only about half sclerotized (ventrally and laterally) in *P. carus* (Figs. 19, 20) but almost fully sclerotized in *P. subreticulata* (Figs. 21, 22). In both, the sclerotized ductus bursae usually looks rather globular in ventral view (Figs. 19, 21); but in *P. subreticulata* it tends—dorso-laterally—to extend backward slightly (and usually to flare slightly) at the ostium bursae (Fig. 21). Genitalic differences between *P. carus* and the superficially distinct *P. rhesus* are much more subtle because in *rhesus*, as in *carus*, the ductus bursae is only about half sclerotized (ventrally and laterally) (Figs. 17, 18). However, the sclerotized ductus bursae looks a little more elongate in *P. rhesus*, especially in ventral view (Fig. 17); and, where it approaches the corpus bursae, the anterior edge of the sclerotization is more irregular in *rhesus* (Fig. 18) than it is in *P. carus* (Fig. 20) (and, for that matter, *P. subreticulata* [Fig. 22]).

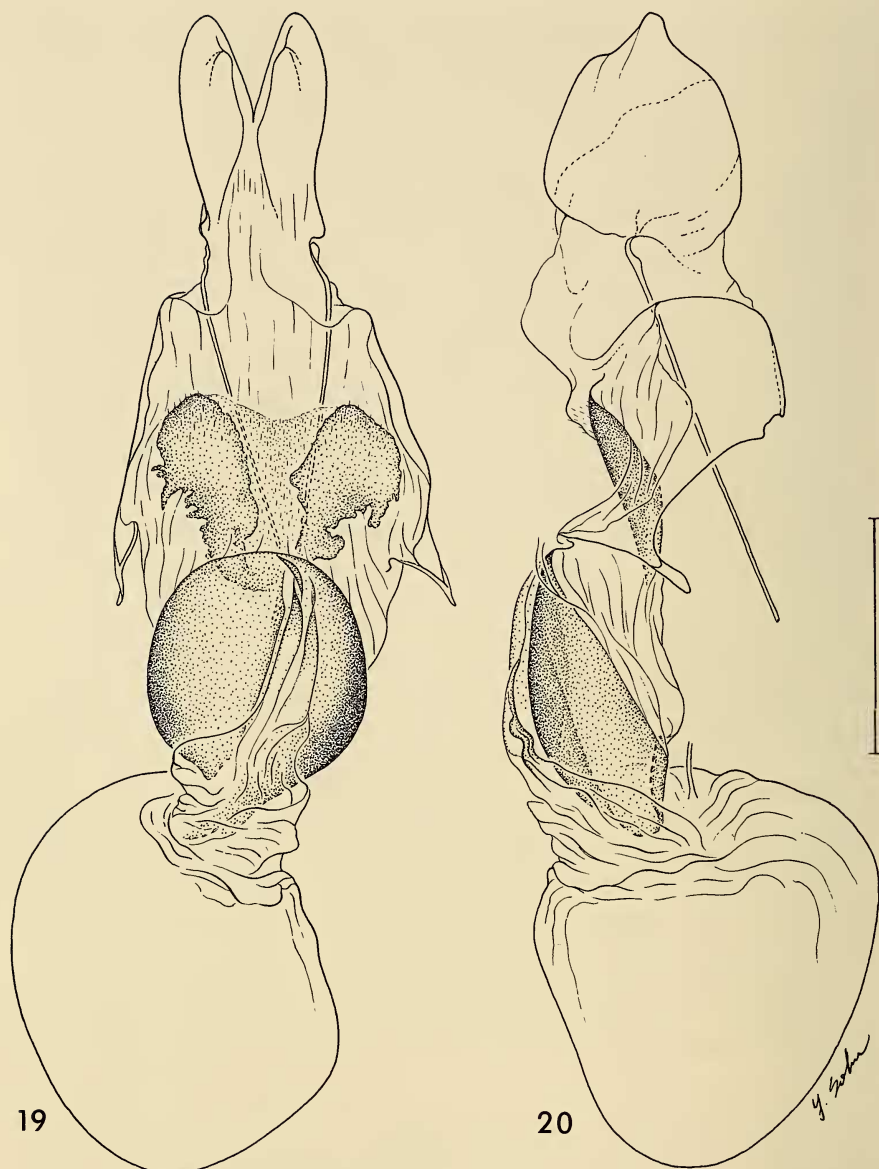
*Polites rhesus* ranges from southern Canada (Saskatchewan and Alberta), in a fairly narrow strip through the western Great Plains and southern Rocky Mountains of the United States (Stanford & Opler 1993), to high mountains of central Mexico (10,000 ft [3050 m] in the state of México); *P. carus*, from the southwestern United States (western Texas to southeastern California—see Stanford & Opler 1993) to central Mexico (Distrito Federal); and *P. subreticulata*, from central Mexico (Sinaloa, Jalisco, Colima, Michoacán, Distrito Federal, Morelos, and Veracruz), through Central America, to Panama (as far, at least, as the Canal).

## DISCUSSION

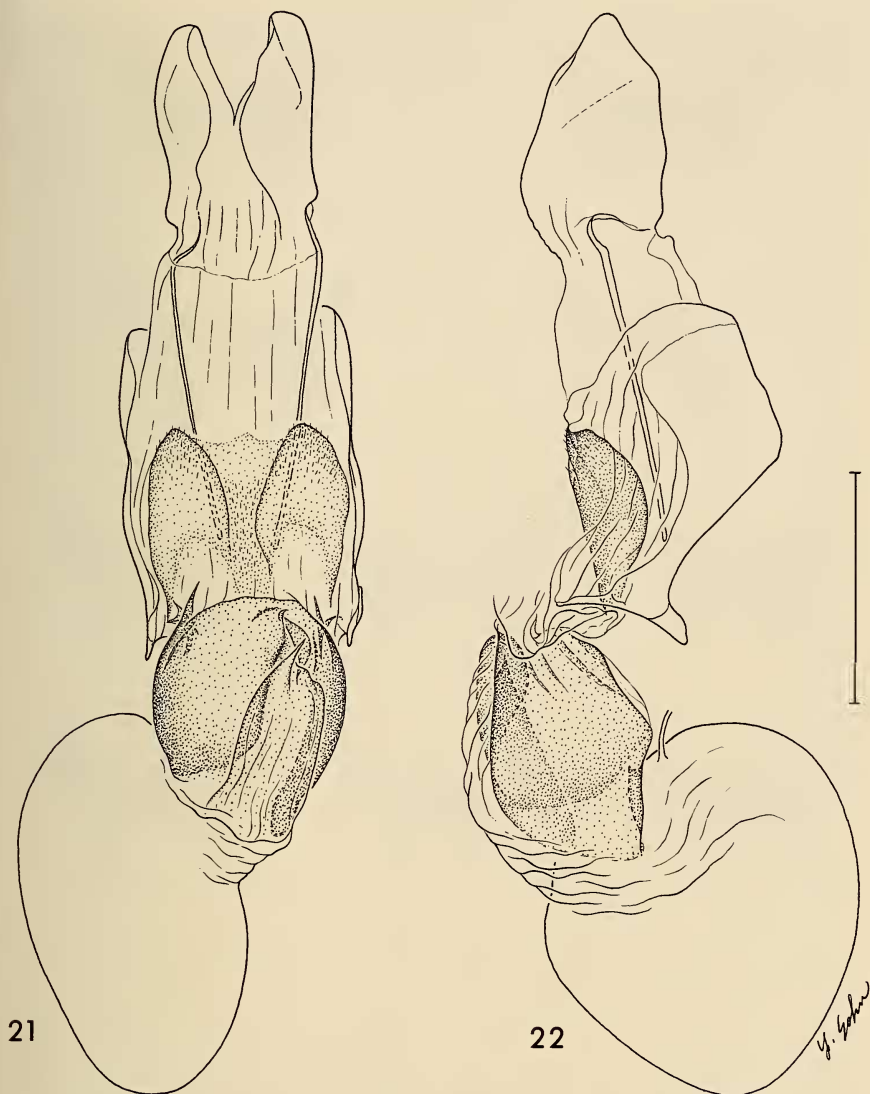
### Generic Limits and Vanishing Traits

Extending generic limits this way calls for more discussion of variation in characters—especially their reduction and loss. The form of the antennal club and the length of its reflexed apiculus, which are widely used in skipper classification, are undeniably valuable. However, though they tend to be conservative at the generic level, they are hardly im-





FIGS. 19, 20. Female genitalia of *Polites carus* from Sunny Glen Ranch, 5000–7000 ft (1525–2135 m), near Alpine, Texas, USA, 1–15 May 1926 [X-3488] (USNM). Scale = 1.0 mm. **19**, Ovipositor lobes (exserted) with apophyses posteriores, eighth tergite with apophyses anteriores (not sclerotically connected to the lamella postvaginalis of the sterigma), sterigma, and bursa copulatrix in ventral view; **20**, The same, plus part of the ductus seminalis, in right lateral view.



FIGS. 21, 22. Female genitalia of *Polites subreticulata* from Mazatlán, Sinaloa, MEXICO, J. A. Kusche [X-3494] (USNM). Scale = 1.0 mm. **21**, Ovipositor lobes (exserted) with apophyses posteriores, eighth tergite with apophyses anteriores (not sclerotically connected to the lamella postvaginalis of the sterigma), sterigma, and bursa copulatrix in ventral view; **22**, The same, plus part of the ductus seminalis, in right lateral view.



23



24



25



26



27



28



29



30



31



32

FIGS. 23-32. Adults of species moved to *Polites* (all  $\times 1$ ) (in USNM unless otherwise indicated); in each figure, upperside on left, underside on right. **23**, *puxillus*  $\delta$ , 28 mi (45 km) E El Salto, 8400 ft (2560 m), Durango, MEXICO, 6-7 August 1972, Vairs & MacNeill (MacNeill collection); **24**, *puxillus*  $\eta$ , 25 mi (40 km) W Durango, 8100 ft (2470 m), Durango, MEXICO, 20 July 1964, J. A. Chemsak [X-3196] (Univ. Calif. Berkeley collection); **25**, *pupillus*  $\delta$ , Sierra de Guerrero, MEXICO, July 1913, R. Müller [X-2699] (type of *Amblyscirtes catahorma* Dyar); **26**, *pupillus*  $\eta$ , 2 mi (3 km) SW Potrerillos, 4200 ft (1280 m), Sinaloa, MEXICO, 7-8 August 1986, J. Brown & Powell [X-3203] (Univ. Calif. Berkeley collection); **27**, *rhesus*  $\delta$ , Sapillo Creek Valley, 5800 ft (1770 m), 12 mi (19 km) N Pinos Altos, Grant Co., New Mexico, USA, 28 May 1959, J. M. & S. N. Burns [X-2712]; **28**, *rhesus*  $\eta$ , Cedar Creek Canyon, 6900 ft (2100 m), Ruidoso, Lincoln Co., New Mexico, USA, 24 May 1959, J. M. & S. N. Burns [X-3504]; **29**, *carus*  $\delta$ , Portal, Chiricahua Mountains, 4800 ft (1465 m), Cochise Co., Arizona, USA, 18 July 1974, J. M. & S. N. Burns [X-2708]; **30**, *carus*  $\eta$ , 6.5 mi (10.5 km) NE Sawtooth Mountain, Davis Mountains, 5600 ft (1705 m), Jeff Davis Co., Texas, USA, 28 April 1959, J. M. & S. N. Burns; **31**, *subreticulata*  $\delta$ , Mexico City, MEXICO, 7 June 1897, O. W. Barrett [X-3498] (forewing with a long tear in space 1b); **32**, *subreticulata*  $\eta$ , Mexico City, MEXICO [X-3491].

mutable. For example, *Amblyscirtes alternata* (Grote & Robinson), which is an *Amblyscirtes* in the narrowest sense, is unique among all those species in having the sizable, delicate, sharp apiculus suddenly reduced to a short, blunt fraction of itself (Burns 1990). Lumping *Yvretta* with *Polites* may bother those who overweigh antennal clubs because the very short but definite apiculus of the rest of *Polites* seems to be lacking in the *rhesus* group. (Its blunt antennal club is one of the main reasons why *Yvretta* was created in the first place and kept well removed from *Polites*.) But in most specimens of each of the species of the *rhesus* group the blunt club actually ends in a slightly reflexed nubbin (comprising a few segments) that looks like a variably vestigial apiculus. A supposedly important difference between the *rhesus* group and the rest of *Polites* becomes relatively trivial.

Differences in stigmal expression are demonstrably insignificant. Although males of *P. carus* and *P. subreticulata* of the *rhesus* group have a fairly well developed, *Polites*-type stigma, males of *P. rhesus* do not: the stigma is, at best, variably vestigial, and is usually missing altogether. In apparent contrast, "real" *Polites* males "always" develop a good stigma—or they did until MacNeill (1993) described *P. norae*, which produces nothing at all. (*Polites norae* is near *P. sabuleti* in the stigmallly well endowed *themistocles* group.) Stigmal expression has been shown to vary in a similar, unpredictable manner within other genera. Despite a respectable male stigma in most species of *Atrytonopsis*, the *lunus* group entirely lacks one (Burns 1982), and *A. deva* (Edwards) "runs a gamut from no stigma, through many and various vestigial and reduced expressions, all the way to the complete three-part structure" (Burns 1982:551).

On the genitalic front, no importance can be attached to the fact that the uncal combs of the *rhesus* group are bigger than those of other *Polites*. They are only about as much larger than those of the *themistocles* and *origenes* groups as those of the *vibex* group are smaller. At the farthest extreme, *Polites* includes *baracoa*, whose uncal combs have vanished without a trace. Moreover, *baracoa* has lost its gnathos. And, in a different kind of unique development, its paired, toothed, caudally-extending titillators have broadly joined each other, near their anterior ends, across the underside of the aedeagus. Altogether, in its genitalic morphology, the *rhesus* group is considerably closer to the *Polites* mainstream than is *P. baracoa*.

Some may be jolted by the broad, round, female-like wings of males of *P. puxillius* (Fig. 23) and *P. pupillus* (Fig. 25) within the *origenes* group, where males of all other species have narrower, more pointed wings than do females. But sexual dimorphism in wingshape (which is typical and extremely widespread in skippers) has abruptly disappeared



elsewhere within the genus *Polites*—in *P. mardon* within the *peckius* subgroup of the *themistocles* group.

### Distribution and Speciation

In the *origenes* group, *P. origenes* (mainly from the eastern and central United States) morphologically and geographically links the northern, transcontinental superspecies *P. mystic* (*P. mystic* and *P. sonora*) and the Mexican sister species *P. pupillus* and *P. puxillus*. These montane sisters appear to be closely allopatric, in part through different altitudinal preferences; but data are too few to say for sure (see Fig. 10). Phylogenetically closer to the Mexican sisters than to superspecies *P. mystic*, *P. origenes* is out of touch with them and broadly sympatric with the superspecies—mostly with *P. mystic* (see maps in Opler & Malikul 1992, Stanford & Opler 1993). However, across all five species of the group, sympatry is limited. Their spatial distribution strongly reflects a set of allopatric speciation events.

In the *rhesus* group, the superficially distinctive and more northward ranging *P. rhesus* extensively overlaps *P. carus* in the southwestern United States and northern Mexico, whereas *P. carus* and *P. subreticulata*, which are sister species, seem (from meager distributional data) almost to replace each other geographically.

Again, the four strictly western members of the *peckius* subgroup of the *themistocles* group—*P. draco*, *P. sabuleti*, *P. norae*, and *P. mardon*—are essentially allopatric (MacNeill 1993). So are several members of the *vibex* group, which Evans (1955) erroneously treated as a single, very widely distributed polytypic species.

All four species groups of *Polites* overlap in distribution, ranging in broadly repetitious—though different—patterns from the neotropics to the nearctic: the *vibex* group from Argentina, Paraguay, Brazil, Bolivia, and Peru to Mexico, the West Indies, and (primarily) the southeastern United States; the *rhesus* group from Panama to southern central Canada; the *origenes* group from southern Mexico to the width of southern Canada; and the *themistocles* group from central Mexico to the width of southern Canada, plus Yukon Territory. But all four species groups of *Polites* still give clear distributional evidence of allopatric speciation within themselves. This is independent evidence that the morphologically defined species groups are correct.

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